TAXONOMY OF THE NARROW-LEAVED VERNONIA OF THE SOUTHEASTERN UNITED STATES[1]

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The narrow-leaved *Vernonia* (i.e., the Angustifoliae and Scaberrimae species groups of Small, 1933) occur on sandy areas from North Carolina into Florida and Mississippi. They were chosen for systematic study because of the conspicuous variability within and among some of the taxa in this group. The usual field and herbarium studies were supplemented by biosystematic investigations.

In the course of this investigation, friendly assistance has been received from many persons. It is not possible to thank them all specifically, but my sincere thanks are none the less real. I am most particularly indebted to Dr. W. H. Duncan (University of Georgia), under whose direction this paper as part of a dissertation was undertaken, for his advice, criticism, and encouragement. The author wishes to thank the curators of the herbaria that kindly lent the specimens of *Vernonia* used in this study. Loans were obtained from the following herbaria: DUKE, Duke University; FLAS, University of Florida; FSU, Florida State University; GA, University of Georgia; GH, Gray Herbarium; MO, Missouri Botanical Garden; NCSC, North Carolina State College; NY, New York Botanical Garden; PH, Academy of Natural Sciences; US, United States National Museum; USF, University of South Florida. Abbreviations are from Lanjouw and Stafleu (1959).

HISTORICAL ACCOUNT

The first description of a narrow-leaved *Vernonia* was by Walter (1788) in "Flora Caroliniana." He applied the name *Chrysocoma graminifolia* Walt. with the description "herbacea, foliis lineari-lanceolatis glabris, floribus corymbofis."

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Michaux (1803) described the same taxon and gave it the name *Vernonia angustifolia* Michx. The second taxon in the group was named and described by Nuttall (1818) as *V. scaberrima* Nutt., noting "Calix (sic) scales filiformly terminated as in *V. noveboracensis.*" Rafinesque (1838) apparently applied the name *V. brevifolia* Raf. to the taxon *V. scaberrima* Nutt.

An erroneous identification of a specimen of *V. angustifolia* Michx. as *V. fasciculata* Michx. by De Candolle (1836) has caused his description of *V. fasciculata* Michx. to be based on a specimen of *V. angustifolia* Michx. (Torrey and Gray, 1841). *V. angustifolia* Michx. and *V. scaberrima* Nutt. were combined by Torrey and Gray (1841) into one species (*V. angustifolia* Michx.).

A third taxon of the narrow-leaved southeastern *Vernonia* was described and named by Chapman (1878) as *V. angustifolia* Michx. var. *pumila* Chapm., from south Florida. Gray (1884) followed the earlier treatment of Torrey and Gray (1841) ; however, he gave varietal status to var. *scaberrima* (Nutt.) A. Gray and listed var. *pumila* Chapm. and var. *texana* A. Gray. This varietal treatment of *V. texana* (A. Gray) Small has caused the appearance of the name *V. angustifolia* Michx. in floras from west of the Mississippi River. This occurred in "Plants of Arkansas" by Branner and Coville (1888) who also changed the name of *V. angustifolia* Michx. to *V. "granienifolia"* (sic) Coville.

Kuntze (1891) changed the generic name *Vernonia* to *Cacalia* and applied the name *C. graminifolia* (Walt.) Kuntze to *V. angustifolia* Michx. A fourth taxon was described from the sand hills bordering the Altamaha River in Liberty County, Georgia, by Small (1898) and named *V. pulchella* Small. Mohr (1901) used the name *V. graminifolia* (Walt.) Mohr for *V. angustifolia* Michx. Although the oldest specific name is Walter's (1788) *graminifolia*, the use of the binomial *V. graminifolia* (Walt.) Mohr in antedated by *V. graminifolia* Gardner, applied in 1847 to a Brazilian species (Gleason, 1906). Small (1903) changed the name and rank of *V. angustifolia* Michx. var. *pumila* Chapm. to *V. blodgettii* Small. Gleason (1906) noted that the use of Chapman's

varietal name for the species is prevented by the publication of the name *V. pumila* Kotschy and Peyr. for an African species.

In 1906, Gleason published "A revision of the North American Vernonieae," listing seven narrow-leaved southeastern species. Included were three new narrow-leaved southeastern *Vernonia* (*V. recurva* Gleason, *V. dissimilis* Gleason, and *V. concinna* Gleason). He separated this group under study into two species groups, Pulchellae and Angustifoliae, based on bract tip shape. In 1922, Gleason used this same treatment in "North American Flora." Small (1933) followed Gleason's (1906) treatment of this group except that he used the name Scaberrimae instead of Pulchellae for one of the species groups. Apparently the last taxonomic shifting was by Schubert (1936) when she placed *V. pulchella* Small as a variety of *V. scaberrima* Nutt.

TAXONOMIC TREATMENT

Benson (1962) stated that any step toward classification of a plant group is an important contribution to knowledge. He also pointed out that the goal of taxonomy is synthesis of data from various fields. Data from several disciplines are used in the following section to clarify fundamental taxonomic problems and to serve as bases for improved classification of the group.

Evolutionary Relationships

The presence of relatively few minor morphological differences is evidence of close relationships among taxa of the group. The taxa considered here apparently diverged from a common ancestor during past geological history, and, except for the allopatric taxon *V. blodgettii* of south Florida, followed this with incomplete merging by the pattern of sympatric introgression. Present evidence does not warrant separation of these taxa into two species groups as did Gleason (1906) and Small (1933).

There is a gap of 80 miles between *Vernonia blodgettii* and those sympatric taxa to the north. This geographic iso-

lation is apparently an effective barrier to gene exchange as its populations show only the minor variation expected in out-crossing population systems. This taxon easily crosses in experimental situations with the other taxa of the study, producing fertile F_1 hybrids. Transplant studies indicated that *V. blodgettii* has a different range of ecological tolerances than the other taxa, thus, perhaps, accounting for its geographic isolation. Morphologically, *V. blodgettii*, is quite distinct. Evaluation of present evidence indicates that this taxon should remain at species rank.

The only confirmed occurrence of *Vernonia pulchella* is in a very limited area of what is known as the Low Terraces in southeast Georgia. It has maintained its identity in this restricted range except for a narrow band at the border of its range where introgression has occurred with *V. scaberrima*. It should be noted that *V. pulchella* differs from *V. scaberrima* in several features such as pubescence, leaf shape, leaf size, leaf texture, size of epidermal cells, compactness of leaf blade mesophyll, and, quite significantly, ecological habitat. Experimental evidence shows that *V. pulchella* is inter-fertile with the other taxa of this study. The resulting F_1 hybrids are vigorous and fertile in all cases. The crosses between *V. pulchella* and *V. scaberrima* resulted in offspring intermediate between the two parents. Ease of experimental hybridizations indicates that isolation is probably ecological. Morphologically, *V. pulchella* is quite distinct. It is concluded that *V. pulchella* should retain species rank.

Examination of the type of *V. recurva* indicated that it is a hybrid between *V. pulchella* and *V. scaberrima* as it only occurs where *V. pulchella* and *V. scaberrima* are sympatric. Artificial crosses of these two taxa produced fertile, vigorous, and intermediate plants closely resembling the type specimen. The backcrosses closely resembled the recurrent parent. Morphological studies of local population samples involving these two taxa substantiated the hypothesis of the hybrid origin of *V. recurva*. The status of *V. recurva* should be altered from species to hybrid. The hybrids may be able to survive due to the presence of a spectrum of

ecological niches between the habitats of the two parents.

The taxa of this study are usually isolated ecologically from the wide-leaved *Vernonia* which occur only in mesic habitats. This isolation is not always effective, and hybridization occurs between narrow-leaved and wide-leaved *Vernonia*. For example, hybridization between *V. angustifolia* and the wide-leaved *V. ovalifolia* in middle Florida has resulted in hybrids previously known as *V. concinna*. Fertile, vigorous, and intermediate artificial hybrids were easily produced in the greenhouse and they were very similar to the type of *V. concinna*. Backcrosses approached the recurrent parent in morphology. Some introgression was indicated from studies of local population samples. The status of *V. concinna* should be altered from species to hybrid.

Introgression of *V. angustifolia* with wide-leaved *V. altissima* in east Alabama and west Georgia has apparently resulted in a form which has been named *V. dissimilis*. In this instance the artificial hybrid was not made; however, crosses of *V. angustifolia* with *V. dissimilis* yielded hybrids closely resembling *V. angustifolia* in most characteristics, as would be expected in a backcross. Also, this hypothesis is supported by the results of detailed analysis of a number of local population samples which indicated introgression. *V. dissimilis*, therefore, should be reported as a hybrid.

Similarly, hybridization was also detected between narrow-leaved *Vernonia* and *V. missurica*, *V. acaulis*, and *V. noveboracensis*, which are wide-leaved species. The presence of these hybrids should be noted; however, it would serve little purpose to name these hybrids and confound the literature, especially since individuals of hybrid origin will continue to be found by field botanists where isolation barriers are broken or incomplete.

The population systems that make up the complex of *V. angustifolia* and *V. scaberrima* are the most extensive and appear to be the most complex of the narrow-leaved *Vernonia*. Present evidence indicates that this complex consists of one variable species consisting of three infraspecific taxa at varietal rank with some local variation. The three varieties are *V. angustifolia* var. *angustifolia* of the Carolinas

and Georgia, var. *scaberrima* of southeast Georgia and southwest South Carolina, and var. *mohrii* of south Alabama, southeast Mississippi, north Florida, and southwest Georgia. The presence of long filiform bract tips and 20-30 flowers per head characterize var. *scaberrima*, while var. *mohrii* is characterized by the presence of bracts with acute to slightly acuminate tips and 8-15 flowers per head and var. *angustifolia* is somewhat intermediate between the two, having acuminate bract tips and 16-20 flowers per head. Although these three varieties are morphologically distinct within their respective centers of distribution, the present data indicate that the taxa are connected by bands of intermediates. In the zones of intergradation characters normally found in the three varieties occur in such combinations that it is frequently difficult to assign a varietal epithet to certain plants.

Artificial crosses between these three varieties produced fertile hybrids, indicating that this could occur in the field. The hybrids are similar to many specimens from the transition zones. Based on observations of herbarium specimens and living material, it appears that backcrossing and subsequent introgression of characters occur at approximately the same rates in both directions. Factors most responsible for keeping these taxa apart are probably ecological in nature.

Three hypotheses should be considered in an attempt to explain the pattern of variation in *V. angustifolia*. The first is mutation, recombination, and natural selection within the taxa. The second is extensive hybridization with repeated backcrossing where the ranges of the taxa overlap, and the third hypothesis is a combination of the first two.

Mutation, recombination, and natural selection could result in the formation of clines of morphological characteristics, as was detected in *V. angustifolia* by utilizing a characteristic-by-characteristic study of local population samples. Stebbins (1950) noted that clines, as contrasted with abrupt changes of morphological features, are probably very common among plant species. Assuming that the ancestors of *V. angustifolia* migrated into the south-

eastern United States via Mexico and Texas, as postulated by Gleason (1923), then clinal or ecotypic variation might be prevalent. This could be due to gene mutation, gene recombination, and natural selection concurrent with migration from one area to another. If natural selection, and not hybridization, is the primary cause of variation in *V. angustifolia*, then gene combinations are a reflection of the environmental conditions or adaptive responses. Mutant genes might drift through the populations and become fixed due to their selective value when the taxa migrated into new or slightly different environments. Stebbins (1950) stated that the direction of evolution is determined largely by the genes accumulated through previous mutations and already present in the population. Natural selection clearly plays an important role in perpetuating accumulated small genetic changes.

The second possible explanation of these morphological clines in *V. angustifolia* is that hybridization occurred in those localities where the varieties are sympatric. Also, it is not enough merely to account for these clines by hybridization alone without including introgression, i.e., gene flow between interfertile taxa through their hybrids by means of repeated backcrossing and selection. The centers of distribution of the three varieties of *V. angustifolia* are probably the Sand Hills of south Georgia, the Fall Line Hills of the Carolinas, and south Alabama, west Florida, and southeast Mississippi. Pleistocene disturbances could have separated the ranges of var. *scaberrima*, var. *angustifolia*, and var. *mohrii*. Later dispersion of these taxa could have allowed hybridization and backcrossing, producing plants intermediate in phenotypic characters where their ranges overlap. The suggestion of hybridization does not preclude that mutation, recombination, and natural selection would not also be present and operative.

It is very difficult to ascribe the variation pattern of *V. angustifolia* with certainty to one or the other of the two hypotheses. Natural selection, although admittedly very important in the evolution of any system of populations

cannot completely account for this type of variation. There is an intergradation of characters between var. *scaberrima* and var. *angustifolia* and also between var. *angustifolia* and var. *mohrii*. In certain portions of the range, namely southeast Georgia, the gradient changes abruptly in respect to some characters. Abrupt changes in gradients of morphological characteristics when not accompanied by correlated changes in the environment are evidence against natural selection and favor the theory of hybridization as the primary cause of the variation patterns in *V. angustifolia*. The problem is further complicated by the location of the center of the range of var. *angustifolia* (which has some characters intermediate between the other two varieties) in the Carolinas and not between the centers of the ranges of the other two varieties. Theoretically, extensive hybridization and backcrossing between taxa over a considerable length of time would produce a broad zone of intermediates between taxa centers. Although the varieties are somewhat variable within their respective centers of distribution, the greatest amount of variation occurs where the ranges overlap. The latter situation, along with the inherent variation, makes a combination of the two hypotheses seem likely, with perhaps more evidence favoring the hybridization hypothesis.

Based on the evidence and conclusions as stated above,

TABLE 1. A comparison of Small's (1933) and the present author's taxonomic concepts of the narrow-leaved *Vernonia*.

Small (1933)	Jones
Scaberrimae	Angustifoliae
V. pulchella	*V. blodgettii*
V. recurva	*V. pulchella*
V. scaberrima	*V. angustifolia*
Angustifoliae	var. *angustifolia*
V. angustifolia	var. *scaberrima*
V. dissimilis	var. *mohrii*
V. concinna	Hybrids
V. blodgettii	*V.* × *recurva*
	V. × *concinna*
	V. × *dissimilis*

the taxonomic status of the narrow-leaved *Vernonia* of the southeastern United States is summarized in Table 1. Also, Table 1 compares the treatment of Small (1933) with that of the present author.

Gleason (1923), in his paper "Evolution and geographic distribution of the genus *Vernonia* in North America", stated that there can be little doubt that the ancestral home of the North American *Vernonia* is tropical South America. Gleason based his conclusions on the existence of diverse and primitive South American species. He also suggested that migration and evolution occurred northward and eastward from Central America, through Mexico and Texas. Evolution following the eastward migration then produced the narrow-leaved taxa of the southeastern United States of this study, which retain the primitive involucre, narrow leaves, and low stature of the Texanae from Texas and Mexico. Wodehouse (1928) confirmed Gleason's hypothesis using pollen morphology.

Recent immigration and incomplete evolution of the taxa were stressed by Gleason. Stebbins (1950), however, noted that speciation usually occurs only on the presence of external or internal isolating mechanisms and that most speciation probably takes place in small populations which are more or less isolated unless there is strong selective pressure. Present evidence indicates that immigration may have been ancient, with isolation and divergence from a common ancestor followed by partial sympatric introgression. This could have led to Gleason's (1923) conclusion, namely, that ". . . they are not easily divided into species groups."

Plants ancestral to the present narrow-leaved *Vernonia* may have reached a variety of sandy ecological niches available in the land mass which is now the southeastern United States. Once established, this ancestor was probably isolated by successive periods of marine invasion of the Pleistocene. Under conditions of isolation, rapid evolution could occur. This is contrary to Gleason's (1923) stress on incomplete evolution rather than isolation pre-

ceding taxa differentiation. The present center of the greatest variation of these taxa in southeast Georgia may be due to the presence of several Pleistocene terraces which permit a variety of ecological niches. Also, the edaphic habitats available for these taxa are not uniform ecologically nor are they continuous in the area. This may explain the incomplete merging of the taxa as indicated by my population studies.

The evolutionary behavior of the allopatric species *V. blodgettii* of south Florida may be attributed to the presence of possible Pleistocene refugia in what is now Florida. These refugia have been discussed by James (1961) in "Endemism in Florida." These refugia might have functioned in providing isolating mechanisms, allowing *V. blodgettii* to evolve from its relatives in response to edaphic or other environmental factors of these Pleistocene refugia habitats of Florida. This may have been followed by migration of the habitat as the sea level receded accompanied by migration of *V. blodgettii* to its present range in south Florida.

Some of the variation necessary for evolution and which according to Stebbins (1950) is to be expected in cross-pollinated populations is evidently present within the populations of *Vernonia.* A possible source of new genes, other than mutation, is introgression with species of wide-leaved *Vernonia,* following partial breakdown of ecological barriers. Since it occurs today, it could have occurred in the past. The long bract tips of several of the taxa, resembling those of *V. noveboracensis* (a wide-leaved *Vernonia),* might have resulted from the inclusion of genes from outside the group. Hybridization experiments carried out to the F_2 and F_3 generations, as suggested by Anderson (1949), might prove fruitful in this area.

Speculation concerning the evolution of a group of taxa should also include possible influences of past changes in the earth's surface and climate. Paleogeologic and paleoclimatic data presented by Schuchert (1935) and Dunbar (1960) indicated that land was available since the Creta-

ceous Period for colonization by *Vernonia* in what is now the southeastern United States. The ancestor of the present taxa, if existent, could have moved into the newly opened habitats during or toward the close of the Cretaceous. Certain *Vernonia* of this group are very abundant on the Cretaceous Fall Line Hills from west Alabama into North Carolina. Isolation of the ancestral populations from those of their own kind to the west could have occurred in the Eocene Epoch by means of the Mississippi Embayment. These early populations (Texanae species group) of the Eocene, if existent, were probably sympatric and morphologically similar.

With the uplift of the Schooley Peneplane and subsequent climatic changes of the Miocene Epoch, along with Oligocene aridity, evolution may have induced a tendency toward Coastal Plain restriction. Isolation of the ancestral populations into small groups probably occurred during the Pleistocene Epoch, due to the formation of geographically separated refugia caused by sea level fluctuations. After the Pleistocene, wide areas were probably opened for colonization and finally migration caused the divergent

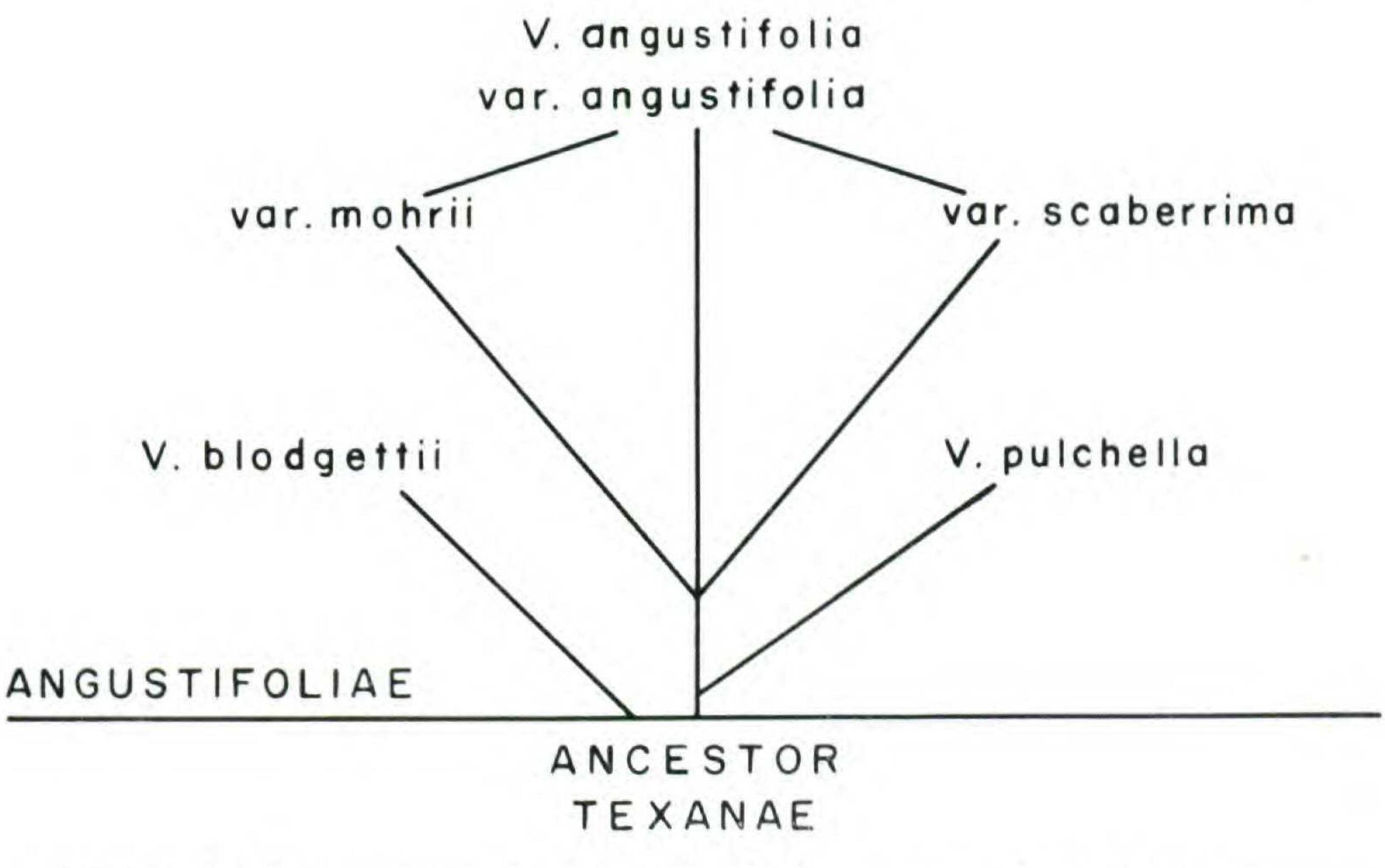

FIGURE 1. Diagrammatic scheme of the supposed phyletic sequence within the narrow-leaved *Vernonia* of the southeastern United States.

taxa to approach a partly sympatric condition, except for *V. blodgettii*. A diagrammatic scheme of the supposed phyletic sequence of the narrow-leaved *Vernonia* is presented in Figure 1.

Systematic Treatment

Small (1933) and Gleason (1906) separated these narrow-leaved *Vernonia* into two species groups; however, due to the many interrelationships of these taxa, I feel that they should be included in one species group (Angustifoliae). The Angustifoliae *Vernonia* are separated from the other southeastern *Vernonia* by their low stature and their characteristically crowded, narrow, linear to oblong-lanceolate or elliptic-lanceolate leaves. They are herbaceous perennials of the Coastal Plain of the southeastern United States.

A list of specimens is not included in this paper but will be prepared in mimeograph form and will be available. The hybrids that have been named are included in this treatment even though I do not believe in naming hybrids. They have been included in order to explain past treatments better.

Key to Species and Named Hybrids

1. Leaves mostly basal, leaf blades smooth and glabrous or nearly so, involucre loosely and irregularly imbricated, pappus light yellow, from the southern one-third of Florida ..... 1. *V. blodgettii*
1. Leaves scattered along stem, leaf blades scabrous to pubescent, involucre closely and regularly imbricated, pappus tawny to purple, not from southern Florida ..... 2.
   2. Cauline leaves narrowly linear or nearly so .... 2. *V. angustifolia*
   2. Cauline leaves elliptic, lanceolate to oblong or oblanceolate .... 3.
      3. Leaves, especially the lower, auriculate at the base, crisped, veins with conspicuous long brownish pubescence beneath .... 3. *V. pulchella*
      3. Leaves not as above ..... 4.
         4. Bract tips over 1.5 mm long ..... 4. *V.* × *recurva*
         4. Bract tips 0.1-0.5 mm long ..... 5.
            5. Leaves lanceolate, scabrous, especially at the margins above, sparsely pubescent below, from east Alabama and west Georgia ..... 5. *V.* × *dissimilis*
            5. Leaves oblanceolate, scabrous to almost glabrous above, almost glabrous below, from northern one-half of Florida ..... 6. *V.* × *concinna*

1. **Vernonia blodgettii** Small, Flora S.E. U.S. 1160. 1903.
Type: Blodgett, (NY). Woods, Pine Key, Monroe County, Florida.
Vernonia angustifolia Michx. var. *pumila* Chapm. Bot. Gaz. 3: 5. 1878.

Stems erect, glabrous, often branched at base, 2-5 dm tall. Leaves mostly basal, 1.8-6.9 cm long, 0.1-1.0 cm wide, linear or nearly so, glabrous above, lightly glandular dotted below, tips obtuse to acute, attenuate at the base, margins slightly revolute, entire. Inflorescence loose, irregular, with few heads. Heads about 21-flowered. Involucre loosely and irregularly imbricated, campanulate, 5.0-8.5 mm high, 5.5-10.5 mm wide. Bracts deltoid to lanceolate, inner 3.9-6.7 mm long, outer 1.7-3.5 mm long, purple, glabrous to slightly pubescent. Bract tips acute to subacute, 0.1-0.5 mm long. Achenes pubescent, ribbed, 2.3-2.7 mm long. Pappus light yellow, bristles 5.5-7.8 mm long, scales irregular, 0.5-0.8 mm long.

Distribution: Southern third of Florida from Indian River, Highlands, and Charlotte Counties south to and including the Florida Keys (see Figure 2).

2. **Vernonia angustifolia** Michx.

Stems erect, pubescent below, sparsely pubescent above, simple to the inflorescence, 4-11 dm high. Leaves crowded, 4-11 cm long, 0.1-0.6 cm wide, linear, scabrous above, scabrous or sparsely pubescent below, tips acute, bases attenuate, margins revolute, entire or with callus teeth. Inflorescence compact to loose and open. Heads 8-30-flowered. Involucre campanulate, 4-10 mm high, 4-10 mm wide. Bracts: inner lance-ovate to lanceolate, outer triangular-subulate to lanceolate, inner 2-8 mm long, outer 1.4-7.0 mm long, purple to greenish, glabrous or puberulent on back, ciliate or entire. Bract tips acute to long acuminate, inner 0.1-4.8 mm long, outer 0.1-5.3 mm long. Achenes pubescent on the ribs, 2.5-3.2 mm long. Pappus tawny to purplish, bristles 5.5-7.0 mm long, scales narrow, 0.4-0.8 mm long.

Distribution: The Coastal Plain of North Carolina, South Carolina, Georgia, and Alabama, the northern half of Florida, and southeast Mississippi.

The tremendous variability of this species has caused much difficulty in plant identification. Lack of an adequate series of specimens and data of an experimental nature has precluded in the past an adequate understanding of this taxon. My results, based on both experimental and morphological evidence, supports the hypothesis that the variability is the result of introgression with related taxa and also the result of natural selection. *V. angustifolia* is

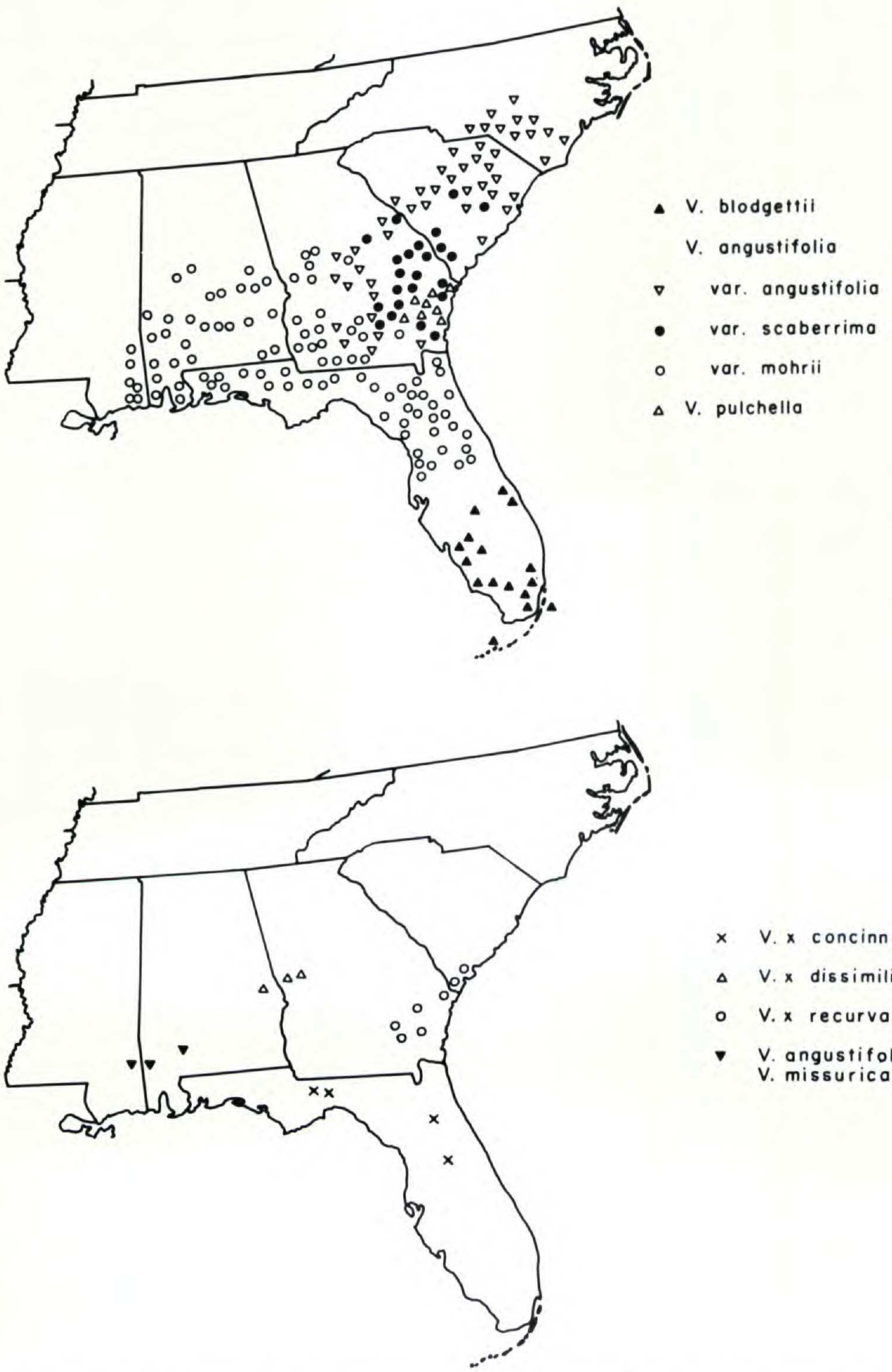

FIGURE 2. Distribution maps of the Angustifoliae species group of *Vernonia*. One dot is plotted every 25 to 30 miles for each taxon. *V. angustifolia* and *V. missurica* frequently hybridize in the area noted on the map.

a variable species consisting of three geographic varieties, with local variation.

Benson (1962) advocates the use of a table rather than keys to segregate varieties of a species. By use of a table, the burden of identification is thrown on a complex of characters rather than on one or two as in a key and it also furnishes a convenient means of character comparison from one variety to the next. The varieties and their contrasting characters are listed in Table 2.

TABLE 2
Characteristics of Varieties of *Vernonia angustifolia*

2a. var. *angustifolia*	2b. var. *scaberrima*	2c. var *mohrii*
Heads 16-19-flowered.	Heads 20-30-flowered.	Heads 8-15-flowered.
Bract tips acuminate to long acuminate, outer 0.3-2.5 mm long, inner 0.1-1.0 mm long.	Bract tips long acuminate, outer 1.5-5.3 mm long, inner 1.4-4.8 mm long.	Bract tips acute to acuminate, outer 0.1-1.2 mm long, inner 0.1-1.0 mm long.
Bracts outer 1.8-4.8 mm long, inner 3.5-7.7 mm long.	Bracts outer 3.9-7.2 mm long, inner 5.0-8.5 mm long.	Bracts outer 1.4-3.9 mm long, inner 2.5-6.5 mm long.
Involucre height 5.0-7.0 mm.	Involucre height 6.5-10.0 mm.	Involucre height 4.0-6.0 mm.
Involucre width 5.0-7.5 mm.	Involucre width 6.0-10.0 mm.	Involucre width 4.0-6.9 mm.

2a. Vernonia angustifolia Michx. var. **angustifolia.**

Type: Not examined (P), Photographs of type (GH, GA).

Vernonia angustifolia Michx., Fl. Bor.-Am. 2: 94. 1803.

Chrysocoma graminifolia Walt., Fl. Car. 196. 1788.

Vernonia fasciculata D.C., Prodromus 5: 63. 1836, not *Vernonia fasciculata* Michx.

Liatris umbellata Bertol., Nov. Comm. Bonon. 8: 79. 1846.

Vernonia granienifolia (sic) Coville, Rep. Geol. Surv., Ark. 4: 189. 1888.

Cacalia graminifolia (Walt.) Kuntze, Rev. Gen. 968. 1891.

Vernonia graminifolia (Walt.) Mohr, Contr. U.S. Nat. Herb. 6: 759. 1901.

Distribution: Southward from Harnett County, North Carolina, along the Fall Line Sand Hills and Coastal Plain into the eastern one-half of the Coastal Plain of Georgia.

This variety is intermediate in certain of its characteristics between var. *scaberrima* and var. *mohrii*. It is characterized by the presence of 16-20 flowers per head, with inner bracts 3.5-7.7 mm long, by inner bract tips 0.1-1.0 mm long, and with involucres from 5.0-7.0 mm high. This taxon is variable and shows evidence of introgression where its range overlaps with related varieties (see Figure 2).

2b. Vernonia angustifolia Michx. var. **scaberrima** (Nutt.) A. Gray, Syn. Fl. N. Am. 1: 91. 1884.
Lectotype: Baldwin (MO).
Vernonia scaberrima Nutt., Gen. 2: 134. 1818.
Vernonia brevifolia Raf., New Fl. 4: 77. 1838.
Vernonia angustifolia Michx. β T. & G., Fl. N. Am. 2: 59. 1841.

The lectotype of var. *scaberrima* was selected from several of the original specimens of this taxon which were studied and annotated by Nuttall. The Baldwin specimen (MO) seemed to best fit Nuttall's description of var. *scaberrima*.

This variety is characterized by the presence of long filiform bract tips, the inner bracts having tips at least 1.5 mm long. The heads are usually 20-30-flowered, the involucre ranges from 6.5-10.0 mm high, and the involucres are from 6.0-10.0 mm wide. Var. *scaberrima* intergrades with var. *angustifolia* and also with *V. pulchella* where it is sympatric with these taxa. Introgressant individuals are difficult to assign to a species or variety as the case may be.

Distribution: Southeast Georgia and to a limited extent in the Coastal Plain of the Carolinas (see Figure 2).

2c. Vernonia angustifolia Michx. var. **mohrii** var. nov.
Type: S. B. Jones 1406 (GA). 12.3 miles north of Citronelle, Washington County, Alabama.

Caulis simplex, erectus, parce pilosus, 4-12 dm altus. Folia crebra, linearia, supra scabra, subtus scabro-pilosa, 4-12 cm longa, 0.1-0.6 cm lata. Corymbus subumbellatus. Capitula cum 8-15 floribus. Involucrum 4.1-7.5 mm altum, 4.0-7.0 mm latum, bractae interiores 2.0-6.3 mm longae, bracteae exteriores 1.4-3.0 mm longae, apex acutus-mucronatus.

Stems simple, erect, sparsely pubescent, 4-12 dm high. Leaves

numerous, crowded, linear, scabrous above, scabrous-pubescent below, 4-12 cm long, 0.1-0.6 cm wide, revolute, frequently with callus teeth. Inflorescence subumbellate. Heads 8-15 flowered. Bracts: inner 2.0-6.3 mm long, outer 0.1-3.9 mm long, usually purple, glabrous or puberulent on the back, ciliate. Bract tips acute to acuminate, inner 0.1-1.3 mm long, outer 0.1-1.5 mm long. Achenes pubescent on the ribs, 2.8-3.2 mm long. Pappus purple-tawny, bristles 4-6 mm long, scales narrow 0.5-0.8 mm long.

This variety is characterized by the presence of bracts with acute to acuminate tips, involucres around 5.5 mm high, and heads with 8-15 (usually 13) flowers per head. Var. *mohrii* intergrades with var. *angustifolia* where these two taxa are sympatric. It also hybridizes with wide-leaved *Vernonia* such as *V. ovalifolia*, *V. altissima*, and *V. missurica* producing local variation and hybrid swarms.

Distribution: Coastal Plain of southwest Georgia, south Alabama, southeast Mississippi, and the northern half of Florida.

3. Vernonia pulchella Small, Bull. Torrey Bot. Club. 25: 145. 1898. *Type*: J. K. Small, (NY). In and about the Altamaha River Swamp in Liberty County, Georgia.

Vernonia scaberrima Nutt. var. *pulchella* (Small) B.G. Schubert, Rhodora. 38: 369-372. 1936.

Stems erect, pubescent below, sparsely pubescent above, simple, 4-7 dm high. Leaves abundant, 2.7-6.0 cm long, 0.5-1.8 cm wide, auriculate at the base, upper leaves narrowed, elliptic-lanceolate to sub-pandurate, scabrous to pubescent above, pubescent below, conspicuous long brownish pubescence on veins beneath, tips of leaves acute, margins revolute and serrate, surface crisped. Inflorescence open, loosely branched. Heads 20-36-flowered. Involucre campanulate, 6.0-10.5 mm high, 5.0-9.1 mm wide. Bracts lanceolate to linear-elliptic, inner 5.0-10.0 mm long, outer 3.0-9.5 mm long, greenish purple, thinly puberulent on back, often ciliate. Bract tips long acuminate, inner 1.3-6.0 mm long, outer 1.1-6.0 mm long. Achenes with pubescent ribs, 2.7-3.1 mm long. Pappus tawny, bristles 5.5-9.0 mm long, scales narrow, 0.6-1.0 mm long.

Distribution: Restricted to a limited area of southeast Georgia on the Low Terraces which extend northeast and southwest of the Altamaha River (see Figure 2).

Introgression occurs between *V. pulchella* and *V. angustifolia* var. *scaberrima* where these two taxa are sympatric around the margins of the range of *V. pulchella*. *V. pul-*

chella has been able to remain distinct in a limited area, probably because of slight differences in the habitat that exclude var. *scaberrima*. A representative sample of the local populations was not available to Schubert (1936) when she changed the rank of *V. pulchella* from species to variety. *V. pulchella* differs in several features such as length and width of the leaves, pubescence of the stem and leaves, margins of the leaves, and size of the epidermal cells.

4. Vernonia × recurva Gleason (pro sp.)

(Vernonia pulchella × V. angustifolia var. *scaberrima)*

Vernonia recurva Gleason, Bull. N. Y. Bot. Gard. 4: 222. 1906. *Type: Harper 2009* (NY). Dry pine barrens near Hortense, Wayne County, Georgia. Isotype (MO).

Stems erect, pubescent, simple, 4-10 dm high. Leaves numerous, 2.5-8.4 cm long, 0.2-0.9 cm wide, lanceolate, scabrous above, scabrous to pubescent below, revolute, margins with scattered callus teeth. Inflorescence open. Heads 19-30-flowered. Involucre campanulate, 6-12 mm high, 5.5-9.0 mm wide. Bracts lanceolate, inner 5-10 mm long, outer 3.0-8.5 mm long, greenish-purple, almost glabrous on back, frequently ciliate. Bract tips long acuminate, inner 1.0-5.0 mm long, outer 1.2-5.7 mm long. Achenes pubescent on the ribs, 2.5-3.5 mm long. Pappus tawny, bristles 5.0-6.5 mm long, scales narrow, 0.6-1.0 mm long.

Distribution: Southeast Georgia and extreme southwest South Carolina on Low Coastal Terraces (see Figure 2).

Vernonia × recurva is found around the edge of the range of *V. pulchella* where *V. pulchella* is sympatric with *V. angustifolia* var. *scaberrima*. Individuals of hybrid origin may survive in nature due to differences in the habitat requirements of the two parents and a spectrum of ecological niches available between these two habitats. Anderson (1949) stated that there must be intermediate habitats for the hybrids to survive, as they tend to be intermediate in habitat requirements.

5. Vernonia × dissimilis Gleason (pro sp.)

(Vernonia altissima × V. angustifolia var. *mohrii)*

Vernonia dissimilis Gleason, Bull. N. Y. Bot. Gard. 4: 224. 1906. *Type: Earle and Baker 1189* (NY). Auburn, Lee County, Alabama. Stems erect, pubescent, simple to the inflorescence, 7-12 dm high.

Leaves 7-13 cm long, 0.5-1.2 cm wide, lanceolate, scabrous above especially near the margin, scabrous and sparsely pubescent below, margins revolute, serrate or with callus teeth. Inflorescence dense with many heads. Heads 10-19-flowered. Involucre campanulate, 3.8-7.3 mm high, 5.1-6.5 mm wide. Bracts ovate-lanceolate to deltoid, inner 3.1-5.5 mm long, outer 1.9-3.3 mm long, purple, glabrous to puberulent on the back, often ciliate. Bract tips acute to acuminate, inner 0.3-1.0 mm long, outer 0.5-1.4 mm long. Achenes pubescent on the ribs, 2.4-3.0 mm long. Pappus tawny to purple, bristles 5.1-6.5 mm long, scales narrow, 0.4-0.8 mm long.

Distribution: Fall Line Hills of east Alabama and the Pine Mountain area in West Georgia (see Figure 2).

6. Vernonia ×concinna Gleason (pro sp.)
(V. ovalifolia × V. angustifolia var. *mohrii)*
Vernonia concinna Gleason, Bull. N. Y. Bot. Gard. 4: 225. 1906.
Type: Nash 1759 (NY). Eustis, Lake County, Florida. Isotype (US).

Stems erect, mostly glabrous, simple to inflorescence, 5-10 dm high. Leaves 7-12 cm long, 0.3-1.3 cm wide, oblong linear to narrowly oblanceolate, scabrous to glabrous above, mostly glabrous below, narrowed to a sessile base, margins revolute, denticulate, entire or with callus teeth. Inflorescence loose. Heads 12-23-flowered. Involucre short-campanulate, 5.2-6.0 mm high, 4.5-6.7 mm wide. Bracts elliptic lanceolate, inner 3.2-4.6 mm long, outer 2.2-3.3 mm long, somewhat loosely imbricated, greenish-purple, glabrous or nearly so on the back, thinly ciliate. Bract tips acute to mucronate, inner 0.1-0.5 mm long, outer 0.1-0.7 mm long. Achenes pubescent on the ribs, 2.5-3.0 mm long. Pappus tawny, bristles 4.6-6.0 mm long, scales narrow, 0.3-0.6 mm long.

Distribution: Infrequent in the northern half of Florida, most common in the Lake Region (see Figure 2).

Literature Cited

Anderson, Edgar. 1949. Introgressive hybridization. John Wiley and Sons, Inc., New York. 109 p.

Benson, L. 1962. Plant taxonomy, methods and principles. Ronald Press, New York. 494 p.

Branner, J. C. and F. V. Coville. 1888. A list of the plants of Arkansas. Ark. Geol. Survey **4:** 189.

Candolle, A. A. de. 1836. Prodromus Systematis Naturalis **5:** 63. Paris.

CHAPMAN, A. W. 1878. An enumeration of some plants, chiefly from the semi-tropical regions of Florida, which are either new, or which have not hitherto been recorded as belonging to the flora of the Southern States. Bot. Gaz. **3:** 5.

DUNBAR, C. O. 1960. Historical geology. John Wiley and Sons, Inc., New York. 500 p.

GLEASON, H. A. 1906. A revision of the North American Vernonieae. Bull. N. Y. Bot. Gard. **4:** 144-243.

———————. 1922. Vernonieae, North American Flora. N. Y. Bot. Gard. **33:** 52-95.

———————. 1923. Evolution and geographic distribution of the genus *Vernonia* in North America. Am. J. Bot. **10:** 187-202.

GRAY, ASA. 1884. Synoptical flora of North America 1: 90-91. New York.

JAMES, C. W. 1961. Endemism in Florida. Brittonia, **13:** 225-244.

KUNTZE, OTTO. 1891. Revisio Generum Plantarum **2:** 968. Germany.

LANJOUW, J. and F. A. STAFLEU. 1959. The herbaria of the world. Regnum Vegatabile **15:** 1-249.

MICHAUX, A. 1803. Flora Boreali-Americana **2:** 94. Paris.

MOHR, C. 1901. Plant life of Alabama. Contrib. U.S. Nat. Herb. **6:** 759.

NUTTALL, T. 1818. The genera of North American plants **2:** 134.

RAFINESQUE, C. S. 1838. New flora and botany of North America 4: 77. Philadelphia.

SCHUBERT, B. G. 1936. Notes on *Vernonia.* Rhodora **38:** 369-372.

SCHUCHERT. C. 1936. Historical geology of the Antillean-Caribbean region. John Wiley and Sons, Inc., New York. 811 p.

SMALL, J. K. 1898. Studies in the botany of the southern United States. Bull. Torrey Bot. Club. **25:** 145.

———————. 1903. Flora of the Southeastern United States, p. 1160, 1161. New York.

———————. 1933. Manual of the Southeastern Flora. Univ. of North Carolina Press, Chapel Hill (reprint). 1554 p.

STEBBINS, G. L. 1950. Variation and evolution in plants. Columbia Univ. Press, New York. 643 p.

TORREY, J. and ASA GRAY. 1841. Flora of North America p. 59. Wiley and Putnam, New York.

WALTER, T. 1788. Flora Caroliniana, p. 196.

WODEHOUSE, R. P. 1928. The phylogenetic value of pollen-grain characters. Ann. Bot. **42:** 891-934.

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